

DROUGHT-INDUCED CHANGES IN WATER RELATIONS IN BROOM SNAKEWEED (*GUTIERREZIA SAROTHRAE*) UNDER GREENHOUSE- AND FIELD-GROWN CONDITIONS

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WAN C., SOSEBEE R. E. and McMICHAEL B. L. Drought-induced changes in water relations in broom snakeweed (*Gutierrezia sarothrae*) under greenhouse- and field-grown conditions. ENVIRONMENTAL AND EXPERIMENTAL BOTANY **33**, 323–330, 1993. Pressure-volume analyses were done on a half-shrub broom snakeweed (*Gutierrezia sarothrae*) subjected to different soil water regimes under pot- and field-grown conditions. Under pot and field conditions, water deficit decreased water and osmotic potentials. In the severely droughted pot-grown plants, osmotic potential at full turgor (Π_{100}) decreased by 0.44 MPa due to reduced symplastic volume, the result of a decreased leaf turgid to dry weight (TW/DW) ratio. A reduction of 0.86 MPa in Π_{100} was observed in the field-grown plants subjected to the first drought cycle, but increased cell wall elasticity occurred in the second drought cycle. The lowered Π_{100} was attributed to osmotic adjustment and reduced symplastic volume. High cell wall elasticity in the second drought cycle led to a greater water loss and tissue desiccation. It is concluded that osmotic adjustment, increased apoplastic water fraction and more rigid tissue are important dehydration-avoidance mechanisms in broom snakeweed.

Key words: *Gutierrezia sarothrae*, osmotic adjustment, acclimation, dehydration-avoidance.

INTRODUCTION

BROOM snakeweed (*Gutierrezia sarothrae*) is a native North American plant ranging from northern Mexico to southern Canada and from Texas to California. In the southwestern United States, broom snakeweed is usually evergreen and has been identified as the main brush and weed problem where it occurs in great densities and abun-

dance. Increased density of the plant has been attributed to overgrazing.^[5] More recently, however, its density is more closely associated with climatic fluctuations rather than overgrazing.^[11,20]

Snakeweed competes with desirable grasses and often becomes dominant on large rangeland areas.^[27] Its efficient use of soil water interferes with the growth of grasses in the arid and semiarid

Abbreviations: Π_{100} and Π_0 , respectively, osmotic potential at full turgor and zero turgor; TW/DW , turgid to dry weight ratio; RWC_0 , relative water content at zero turgor; E , bulk modulus of elasticity; P , bulk turgor pressure; W_a and W_s , respectively, relative water fraction of tissue apoplasm and symplasm; W_p/W_s , ratio of symplastic water loss at zero turgor to the total symplastic water.

rangelands.¹²⁶ Snakeweed has a shallow fibrous root system and the roots can access water and nutrients at the same soil depth as most perennial grasses.¹⁹ However, during a summer drought, when leaves of most grasses are rolled, snakeweed leaves remain turgid, actively growing along with honey mosquito (*Prosopis glandulosa*)—the most drought-resistant species in the southwestern rangelands.

In American cold desert, DePUIT and CALDWELL¹⁷ found that snakeweed had higher stomatal conductance and photosynthetic rates than the drought-resistant true shrub *Artemisia tridentata*. Snakeweed also exhibited less stomatal control of water loss than *Artemisia* and shed leaves during the drought period. Under water deficit, snakeweed had lower plant water potentials than *Artemisia*.¹⁷ Major die-off of snakeweed occurred in the extreme summer drought of 1984 in New Mexico rangelands,¹⁹ but die-off has rarely been observed during a spring drought.

HSIAO *et al.*¹⁰ found that leaf rolling in rice plants can be delayed by osmotic adjustment. The maintenance of turgidity of snakeweed leaves during soil drying might also be related to the same mechanism. The lower water potential in snakeweed under water deficit¹⁷ may indicate a lower solute potential which could result from reduced symplastic volume and/or osmotic adjustment. It seems likely that changes in water-relation parameters are involved in drought-resistance mechanisms in snakeweed. However, HINCKLEY *et al.*¹⁸ questioned the importance of osmotic adjustment for woody plants. Snakeweed is an important drought-resistant plant species, yet little is known about its water relations. Our objective was to test the hypothesis that osmotic adjustment and changes in water-relation parameters are dehydration-avoidance mechanisms in snakeweed subject to drought.

MATERIALS AND METHODS

The study was divided into two parts. A field study was initiated in April 1991 and concluded in July 1991 on the Texas Tech University campus in Lubbock, TX. Soil on the site is an Amarillo fine sandy loam (fine-loamy, mixed, thermic Aridic Paleustalfs). The climate of Lubbock is semiarid with an annual precipitation of 450 mm.

Monthly and annual precipitation is quite variable. Usually little precipitation occurs in the early spring; therefore, the native plants are subjected to water deficit when growth begins in mid-April to mid-May. In 1991 the rainy season occurred between mid-May and late June, followed by a drought period in July. The snakeweed plants selected for study were grown in a native rangeland.

In a greenhouse study, mature snakeweed plants were transplanted into 19-l plastic pots which were 30 cm high and 29 cm in diameter. The pots were filled with Amarillo fine sandy loam. The plants were grown in the greenhouse environment weeks before the experiment began. Seventy-two plants were randomly divided into three groups which were subject to three different irrigation treatments: (1) watered (WW) to field capacity twice a week; (2) moderately stressed (MS) and (3) severely stressed (SS). Treatments MS and SS, respectively, received 50 and 25% of the irrigation quota of treatment WW.

Six foliated twig samples for pressure-volume (PV) analysis were collected in each treatment; one from each individual plant approximately 40 days after the plants had been subject to the above treatments in the greenhouse study. The plant samples in the field study were collected once every 4 weeks from mid-April to mid-July (the vegetative growth stage). Six samples were taken at 8.00 a.m. at each collection period. All twig samples were sealed in humidified plastic bags, and brought to the laboratory as rapidly as possible. The twigs were recut under distilled water, put into plastic bags, and kept in a dark cabinet for 3 hr to rehydrate. The rehydrated twig was weighed with an analytical scale, and water potential was determined with a Scholander-type pressure chamber. Fresh weights of the twig were obtained before and after each determination of water potential was made on the twig. For water potential determination, the pressure chamber was pressurized and depressurized slowly (less than 0.3 MPa per min). The water expressed at each measurement was collected for 10 min with a piece of filter paper. The pressure chamber and the analytical scale box were lined with wet paper towels to keep a high relative humidity in the chamber and the scale box. The pressure increment at each determination of water poten-

tial was 0.3 MPa and the maximum pressure applied to the twig was 4–4.5 MPa. At the end of the dehydration procedure, the twig was oven-dried at 75°C for 24 hr for determination of its dry weight.

Relative water content (RWC) was determined following the method of BARRS and WEATHERLEY.⁽²⁾ Relative water content was plotted against the inverse of water potential and a linear regression fitted to the linear segment of the curve at which bulk turgor pressure became zero. The goodness of fit was evaluated based on the correlation coefficient (r) and the linear regression with the highest r value being used in each individual analysis. For most of the data $r > 0.98$ was obtained for the linear regression lines.

Tissue osmotic potential at full turgor (Π_{100}) and zero turgor (Π_0), relative water fraction of the tissue apoplast (W_a) and symplast (W_s) were determined from the PV curves.^(24,25) The bulk modulus of elasticity (E) was defined as $dP \cdot V / dV$,⁽²⁵⁾ where dP is the change in turgor pressure for a change in cell volume (V) or tissue water content. Bulk modulus of elasticity was calculated according to the equation $E = \tan a \cdot RWC_0$,⁽²⁸⁾ where $\tan a$ is the slope between P (turgor pressure) and RWC ; RWC_0 is the RWC at zero turgor.

At each sampling date, dawn and midday water potential measurements were taken with a pressure chamber on the same sampling plants. Osmotic potential was calculated from the PV curves.⁽²⁵⁾

The complete randomized design was used in the experiments. The data were subjected to analysis of variance, mean separation tests (Fisher's LSD) and correlation analyses with a Statistical Analysis System (SAS) computer program.

RESULTS

In the field and greenhouse studies, water and osmotic potential decreased as soil dried (Figs 1 and 2). These figures also show that zero turgor potential occurred at midday during May and July droughts (Fig. 1), and in MS and SS treatments (Fig. 2), indicating that snakeweed can tolerate tissue desiccation. The osmotic potential at full turgor and Π_0 decreased as apoplastic water fraction (W_a) increased (Tables 1 and 2).

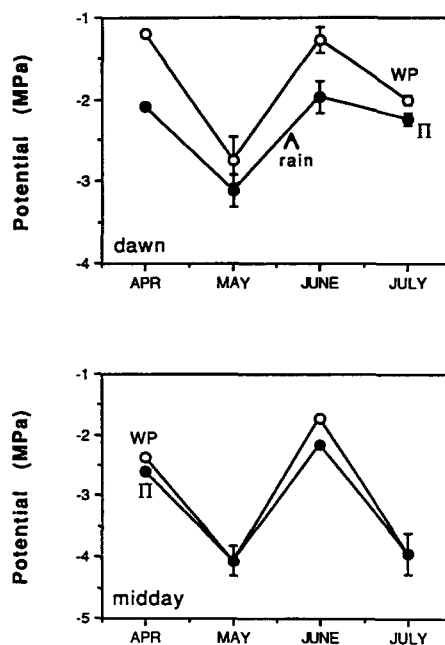


FIG. 1. Plant water potential (WP) and osmotic potential (Π) of broom snakeweed grown in the field and measured at dawn and midday. Each datum point is an average of three to four replications. The vertical bars represent ± 1 S.E.

The declines in Π_{100} and Π_0 have been described as an adaptive mechanism to water deficit,^(22,25) because it can help the plant to maintain a water potential gradient and thus water flux from the soil to the plant as the soil dries. Apoplastic water fraction was significantly higher (0.507, $P \leq 0.05$) in the SS pot-grown plants and the field-grown plants in the droughted May (Tables 1 and 2). Also, Π_{100} and Π_0 were both negatively correlated with W_a (Tables 3 and 4). This indicates that increased W_a could at least partially explain the observed decline in Π_{100} .^(17,25) When snakeweed suffered water deficit, some symplastic water would be redistributed to apoplast, and Π_{100} and Π_0 decline as a result of reduced symplastic volume.

Apoplastic water fraction was highly correlated with RWC_0 in field- and pot-grown plants (Tables 3 and 4). For every unit decline in water potential, there was a small reduction in water content in

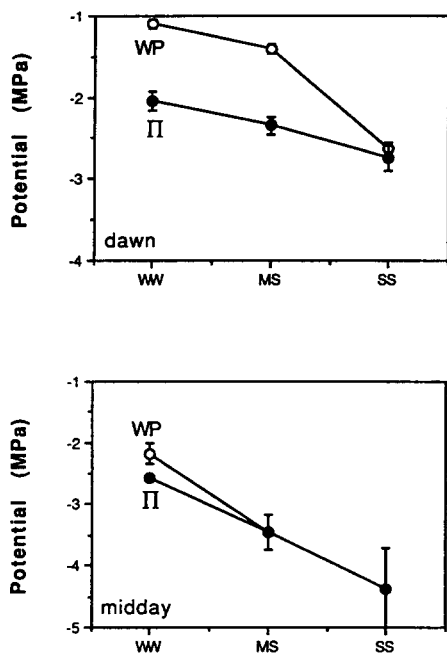


FIG. 2. Plant water potential (WP) and osmotic potential (Π) of broom snakeweed grown in the pots. Each datum point is an average of three to four replications. The vertical bars represent ± 1 S.E. WW, Well-watered; MS, moderately stressed; SS, severely stressed.

the water-stressed plants (Fig. 3). A similar relationship also occurred in the field-grown plants (data not shown).

The leaf turgid weight to dry weight (TW/DW) ratio declined as water stress intensified in the pot-grown plants (Table 2). The reduction in TW/DW ratio indicates greater cell wall thickness and rigidity.⁽¹²⁾ Strong negative correlations between TW/DW and W_a were found in field- and pot-grown plants (Tables 3 and 4), suggesting that an increase in W_a was due to greater cell wall materials when subjected to water stress.

The ratio of symplastic water loss at zero turgor to the total symplastic water (W_p/W_s) was highly correlated with Π_{100} , E and RWC_0 (Tables 3 and 4). More elastic tissue (smaller E) lost a greater percentage of symplastic water, and had a lower RWC_0 . More water was lost from the symplasm at zero turgor in field-grown plants in June and

July than in April and May (Table 1) because of more elastic tissue.

TW/DW and E in the pot-grown plants showed a significant negative correlation ($r = -0.65$, $P \leq 0.05$, Table 4) suggesting that TW/DW is related to rigidity of cell walls. TW/DW is also significantly correlated with Π_{100} and RWC_0 in the pot-grown plants (Table 4). A decrease in Π_{100} of 0.44 MPa was observed in pot-grown plants subject to severe water stress as compared to the well-watered plants probably due to a decrease in TW/DW (Table 2). Neither Π_{100} nor E was correlated with TW/DW in the field-grown plants (Table 3), which agreed with the work of RASCIO *et al.* on wheat.⁽²¹⁾ However, Π_{100} in the snakeweed during the drought in May was 0.86 MPa ($P \leq 0.05$, Table 1) lower than that in June which was wet.

Hofler diagrams relating relative symplastic water loss to bulk turgor pressure, bulk osmotic potential and water potential for May and July (Fig. 4) indicate that turgor pressure was maintained mainly by a lower Π_{100} in the first drought cycle (May), but by increased cell wall elasticity in the second drought cycle (July). Without the seasonal adjustment in Π_{100} , positive turgor pressure would not have been possible in May, because the water potential at dawn was -2.75 MPa (Fig. 1), which was lower than Π_0 in April (-2.51 MPa, Table 1). In July, turgor pressure declined slowly as water potential decreased mainly due to increased tissue elasticity (lower E , Table 1).

DISCUSSION

Under conditions of water deficit, pot- and field-grown plants increased the apoplastic water fraction (from 0.20 to 0.50). CUTLER *et al.*⁽⁶⁾ found that a high apoplastic water content is often associated with drought-adapted plants. Π_{100} declined as tissue symplastic volume reduced in pot- and field-grown plants. But in the field-grown plants the reduction of Π_{100} in May (0.86 MPa) was nearly one-fold greater than that (0.44 MPa) in the severely stressed pot-grown plants, indicating that net solute accumulation contributed substantially to the reduction in Π_{100} .

HINCKLEY *et al.*⁽⁸⁾ found that osmotic adjustment is of minor importance as a mechanism in

Table 1. Water relation parameters of field-grown broom snakeweed plants

	Π_{100}	Π_0	TW/DW	RWC_0	E	W_a	W_p/W_s
April	-1.99a	-2.51a	3.14a	0.826a	9.68a	0.212a	0.222a
S.D.	0.05	0.015	0.09	0.012	0.75	0.017	0.011
May	-2.71b	-3.33b	2.37b	0.888b	19.36b	0.508b	0.227a
S.D.	0.05	0.236	0.173	0.026	10.33	0.068	0.037
June	-1.85c	-2.61a	2.56b	0.784a	5.72a	0.219a	0.300c
S.D.	0.09	0.24	0.29	0.046	2.05	0.120	0.042
July	-1.74c	-2.60a	2.29b	0.778a	6.41a	0.336a	0.334c
S.D.	0.11	0.17	0.01	0.044	3.52	0.116	0.023

S.D., Standard deviation. Means within the same column followed by the same letter are not significantly different ($P > 0.05$, Fisher's least significant difference test).

Table 2. Water relation parameters of pot-grown broom snakeweed plants

	Π_{100}	Π_0	TW/DW	RWC_0	E	W_a	W_p/W_s
WW	-1.91a	-2.37a	3.74a	0.776a	4.71a	0.192a	0.267a
S.D.	0.164	0.153	0.24	0.011	0.355	0.007	0.018
MS	-2.23b	-2.82b	3.07b	0.836ab	9.88a	0.234a	0.213a
S.D.	0.04	0.02	0.13	0.029	2.20	0.119	0.009
SS	-2.35b	-3.04c	2.88b	0.891b	33.44b	0.507b	0.192a
S.D.	0.213	0.16	0.20	0.059	16.32	0.127	0.075

S.D., Standard deviation. Means within the same column followed by the same letter are not significantly different ($P > 0.05$, Fisher's least significant difference test).

Table 3. Correlation coefficients in water relation parameters of the field-grown broom snakeweed plants

	Π_{100}	Π_0	TW/DW	RWC_0	E	W_a	W_p/W_s
Π_{100}		0.84†	ns	-0.82†	-0.77†	0.69†	0.67†
Π_0			0.50*	-0.55*	-0.72†	-0.81†	ns
TW/DW				ns	ns	-0.55*	ns
RWC_0					0.83†	0.57*	-0.76†
E						0.67†	-0.64†
W_a							ns

ns, Non-significant, * $P \leq 0.05$, † $P < 0.01$ (Pearson correlation procedure).

the drought resistance of four shrub species (*Olea europaea*, *Crataegus monogyna*, *Sorbus aria* and *Viburnum lantana*). In this study, however, the decrease in Π_{100} in the field is 0.86 MPa, which is substantially higher than the 0.5 MPa for the evergreen desert species *Larrea tridentata* and *Atriplex polycarpa*.⁽¹³⁾

Osmotic adjustment is greater when some plants suffered slow rates of stress development as compared with rapid ones.⁽²²⁾ Soil drying is slow

in the field, but rapid in pots. There is always some water that can be extracted from the subsoil to compensate for the high cost of osmotic adjustment.⁽²⁵⁾ While in the severely stressed pot-grown plants, the available soil water is very limited, and it is not worthwhile for the plant to invest its energy in a process which is unlikely to do more good than harm.

There was no osmotic adjustment in the field-grown plants during the second drought cycle in

Table 4. Correlation coefficients in water relation parameters of the field-grown broom snakeweed plants

	Π_{100}	Π_0	TW/DW	RWC_0	E	W_a	W_p/W_s
Π_{100}		0.72*	0.74†	-0.87†	-0.73*	-0.59*	0.83†
Π_0			0.81†	-0.65*	ns	-0.68*	ns
TW/DW				-0.85†	-0.65*	-0.73*	0.71*
RWC_0					0.90†	0.83†	-0.90†
E						0.79†	-0.86†
W_a							ns

ns, Non-significant, * $P \leq 0.05$, † $P < 0.01$ (Pearson correlation procedure).

July (Table 1). This is in contrast to the results as reported by BENNETT and MOONEY for *Larrea* and *Artriplex* species,⁽³⁾ BOWMAN and ROBERTS for evergreen chaparral shrubs,⁽⁴⁾ and MYERS and NEALES for *Eucalyptus* species.⁽¹⁵⁾ These authors found that osmotic potential tended to decrease throughout the summer period or during the second drought cycle. Loss of capacity for osmotic adjustment has been attributed to aged leaves⁽¹⁴⁾ which are often associated with decreased photosynthetic capacity and reduced supply of assimilates. Our unpublished data indicate that as much as 20% of leaf area reduction occurred from June to July. In addition, the rapid stem elongation in July^(16,19) demands great export of assimilates from the photosynthetic tissue, which

means that little of the assimilates was available for osmotic adjustment.

Perhaps the most interesting phenomenon in this study is that the plants responded differently to drought in the early growing stage (May) than in the later stage (July). The bulk modulus of elasticity was high in May (19.36 MPa, Table 1), then declined in the rainy period (June, 5.72 MPa, Table 1) and remained low in the subsequent drought period (July, 6.41 MPa, Table 1). MYERS and NEALES⁽¹⁵⁾ suggested that three *Eucalyptus* species have more elastic tissue when subjected to a second drought cycle. TURNER and JONES⁽²²⁾ found reduced cell size and more elastic cells linked to the low TW/DW ratio under conditions of water deficit. As the plants suffered the second drought, the cells became smaller (low TW/DW ratio, Table 1) which can lead to more elastic cells.

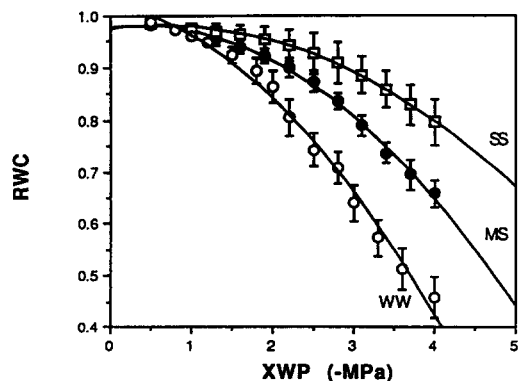


FIG. 3. Relationship between relative water content and water potential for three treatments in the pot study. Each datum point is an average of four to six replications. The vertical bars represent ± 1 S.E. WW, Well-watered; MS, moderately stressed; SS, severely stressed.

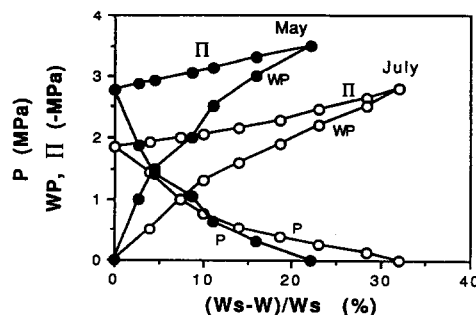


FIG. 4. Hofler diagrams relating relative symplastic water loss $(W_s - W)/W_s$ to bulk turgor pressure (P), bulk osmotic pressure (Π) and water potential (WP) in the first (May) and second (July) drought cycles in the field-grown snakeweed plants.

The more elastic tissue in July may help the plant to sustain growth by maintaining a positive turgor pressure (Fig. 4), but it can also expose the plant to a great risk of tissue desiccation. At zero turgor, 30% more water was lost from the symplasm in June and July than in April and May (Table 1). A greater water loss in June was balanced by a rapid water uptake from the wet soil, but not during the droughted July. In July, we repeatedly observed death or quiescence of some plants from soil water deficit. BARNES *et al.*⁽¹⁾ found that ozone and/or acid mist markedly increased tissue elasticity of Norway spruce (*Picea abies*) and enhanced the sensitivity of the trees to drought damage.

Because of less stomatal control over its water loss,⁽⁷⁾ the plant often could not keep its water balance during the high evaporative demands of July and the water potential dropped to -4 MPa or below in the afternoon (Fig. 1). With the elastic tissue, -4 MPa is equivalent to a *RWC* of 53.8% ($\pm 3\%$ S.E., $n = 6$, data not shown). In the plants which later died, we observed a *RWC* of 50% ($\pm 2.8\%$ S.E., $n = 6$) just before plant death. HINGKLEY *et al.*⁽⁹⁾ found that the water potential at which irreversible cell damage occurred was -4.9 MPa for six deciduous shrub species and the corresponding *RWC* ranged from 45.7 to 62.7%. In the samples taken in broom snakeweed in July, when balance pressure in the pressure chamber increased to 4.3–4.5 MPa, and *RWC* dropped to 52–46%, the data points deviated from linearity. According to TYREE *et al.*,⁽²³⁾ this indicates tissue death.

In contrast, a water potential of -4 MPa in May corresponds to a *RWC* of 82.5% (± 0.028 , $n = 6$, data not shown). Although May was a very dry month (dawn water potential -2.75 MPa, Fig. 1), no single plant died or became quiescent. A similar phenomenon occurred in the severely stressed pot-grown plants (Fig. 3). HSIAO *et al.*⁽¹⁰⁾ found that osmotic adjustment delayed leaf senescence and tissue death in rice plants. Osmotic adjustment and/or increased W_a apparently contributed to the survival of the snakeweed plants subjected to drought. Both of these mechanisms can help the plant to maintain a steeper water potential gradient from soil to plant with a relatively small decrease in water content as shown in Figs 3 and 4. These mechanisms, therefore,

represent an important drought acclimation in the snakeweed plant. Plant death or quiescence in July was probably due to a lack of these mechanisms, since water stress was no more, if not less, severe in July than in May (Fig. 1).

PIEPER and McDANIEL⁽¹⁹⁾ stated that “in spite of its competitive characteristics, broom snakeweed appears to be susceptible to drought damage”. With more elastic cell walls, the snakeweed plant can maintain a fast growth rate in the summer,^(16,18) which makes it more competitive, but also makes it susceptible to drought damage. Therefore, we conclude that in addition to osmotic adjustment, the increased apoplastic water fraction and more rigid tissue, characterized by more water tightly bound to the cell walls, are important dehydration-avoidance mechanisms in broom snakeweed.

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